Allowing species to constantly change their positions in the food web: initial sequence still matters

Jade, Mar 27

One important question left in the previous food web construction model is that: what if species are not fixed to their trophic level chosen when entering the community, but instead are free to change to other trophic levels later when the comparative advantage changes (due to the addition of new species). Here I am going to show the patterns derived from this more realistic assumption, from which we can make inference about the dynamic stability of any given food web structure. The result also suggests the likely existence of two or more alternative stable structures for the food web given the species composition. In one word, the sequence in which species are added affects both the dynamics and the stable structure of the food web.

Throughout, "trophic leap" is defined as the repositioning of an old species to a trophic level different from the one it chose when entering the community.

1 When does trophic leap happen

Starting with an optimal food web, i.e. a food web where every species is in its most advantageous trophic levels and any trophic leap does not increase its steady state abundance. Now a new species is added. Through the procedure illustrated in the last write-up, it is added to trophic level i where it has the maximum steady state abundance. Due to the addition of the new species, some old species might have higher advantage at a different trophic level other than the one it is in. Therefore the food web is not optimal any more and there is a potential for it to transform by trophic leaps of those not optimized species. To see how this happens, the first question is to identify the old species that are motivated for trophic leaps.

First it is easy to see that all species from other trophic levels ($\neq i$) are not motivated for trophic leaps, since neither the species compositions nor the resource constraints of those trophic levels are changed by the addition of the new species.

So the motivated species can only be from trophic level i. Before adding the new species, all species at trophic level i were at their most advantageous positions. The question is whether this changes with the addition of the new species. Although some intuitive inferences could be made (will be discussed later), the most general answer has to be obtained by recalculating the comparative advantage for each of these species with the new species added. In the following I introduce a new method to construct a food web where any trophic leap by an old species that increases its steady state abundance is allowed.

2 Trophic leap algorithm

To add a new species into the community, follow these steps:

1) Add it to its optimal trophic level (i) based on the structure of the current food web;

2) For all species in trophic level i, first drop it from the food web (with the new species added), then recalculate the comparative advantage of it at all trophic levels, from which we get its updated optimal trophic level j;

3) For all species with $j \neq i$, starting from the smallest one of them (will be explained later), move it to its optimal trophic level and recalculate the j for the rest;

4) Repeat step 3) until all species are in their optimal trophic levels.

In step 3) I assume trophic leap to happen from the smallest motivated species to make the number of trophic leaps as small as possible. This is because the leaving of a smaller species lifts more of the competition pressure among species in that trophic level compared to the leaving of a bigger species, and therefore reduces the motivation for trophic leaps of the remaining species.

Notice that the above procedure is recursive in that the trophic leap in step 3 involves the whole process from step 1 - 4. To reveal what sequence of adding species is the most stable through time, I keep a record of the number of trophic leaps (how many times step 3 is conducted) until a stable structure is reached.

For all following analyses, $R = 10, \tau = 0.1, S_0 = 100$, θ is drawn from a geometric distribution ($p = 0.2$).

3 Resut

In all of the figures, a) and c) show the food web structure, b) and d) show the variation of mean body size across trophic levels; a) and b) are patterns before trophic leaps (as in the last write-up), c) and d) are patterns after trophic leaps. The number of trophic leaps is shown below the x-axis (annotated by nrep=) in graph c).

3.1 $D_r = 0$

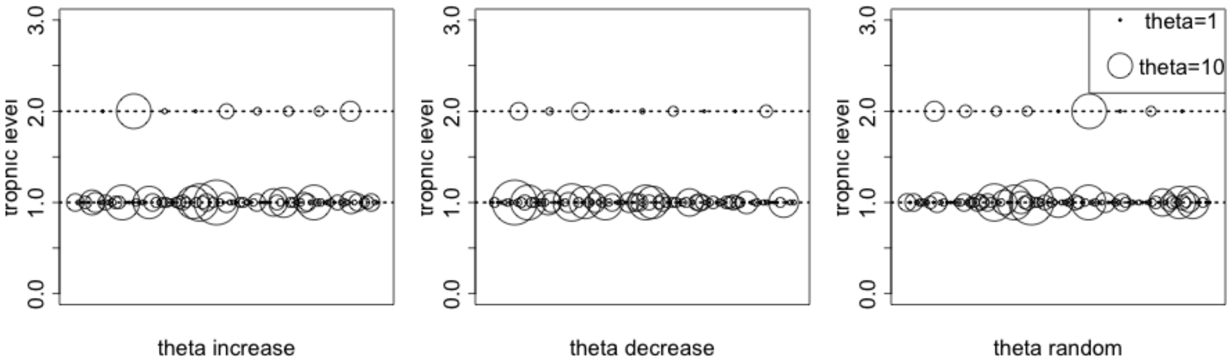

Figure 1. a) Food web structure, before trophic leaps ($D_r = 0$)

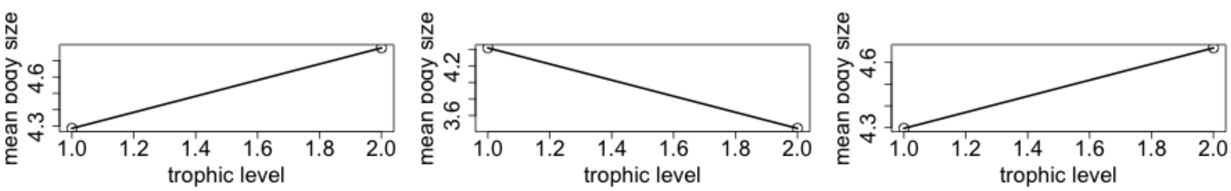

Figure 1. b) Mean body size variation across trophic level, before trophic leaps ($D_r = 0$)

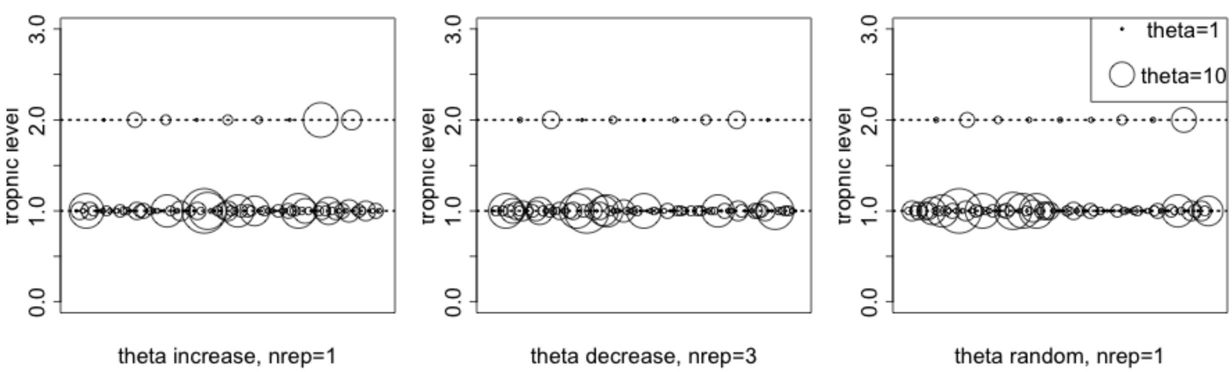

Figure 1. c) Food web structure, after trophic leaps ($D_r = 0$)

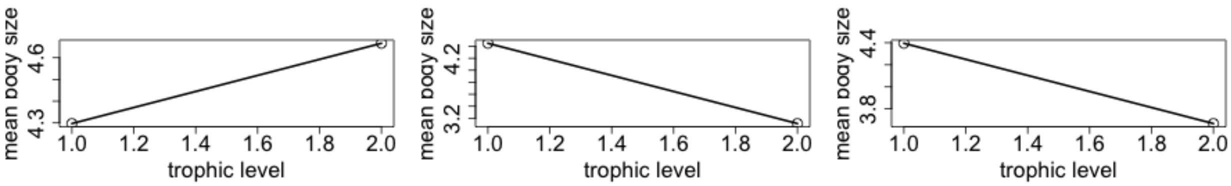

Figure 1. d) Mean body size variation across trophic level, after trophic leaps ($D_r = 0$)

3.2 $D_r = 0.5$

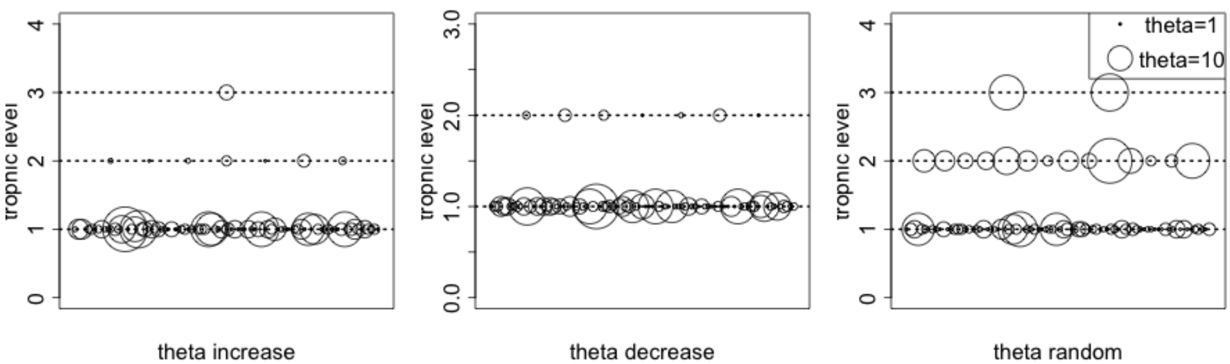

Figure 2. a) Food web structure, before trophic leaps ($D_r = 0.5$)

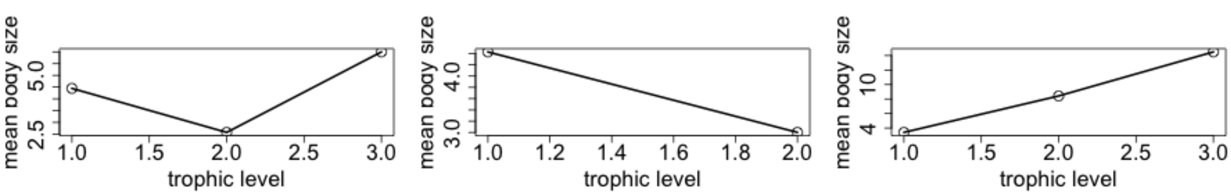

Figure 2. b) Mean body size variation across trophic level, before trophic leaps ($D_r = 0.5$)

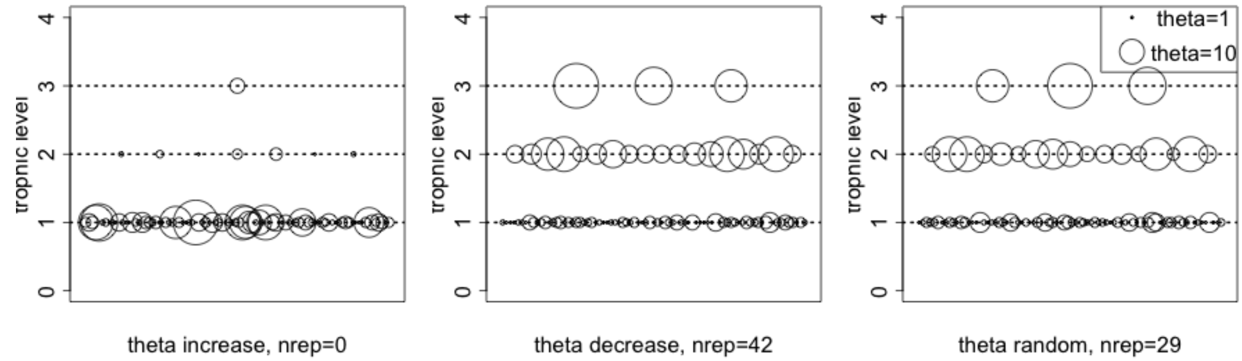

Figure 2. c) Food web structure, after trophic leaps ($D_r = 0.5$)

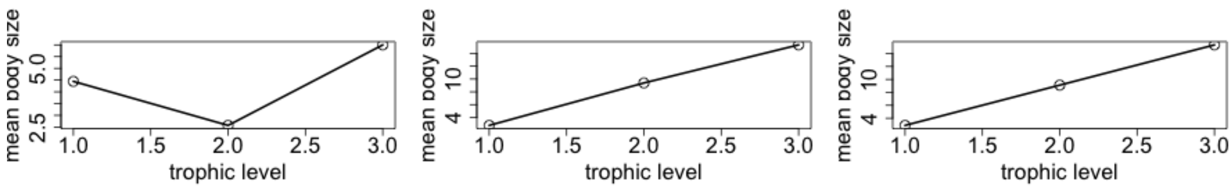

Figure 2. d) Mean body size variation across trophic level, after trophic leaps ($D_r = 0.5$)

3.3 $D_r = 0.7$

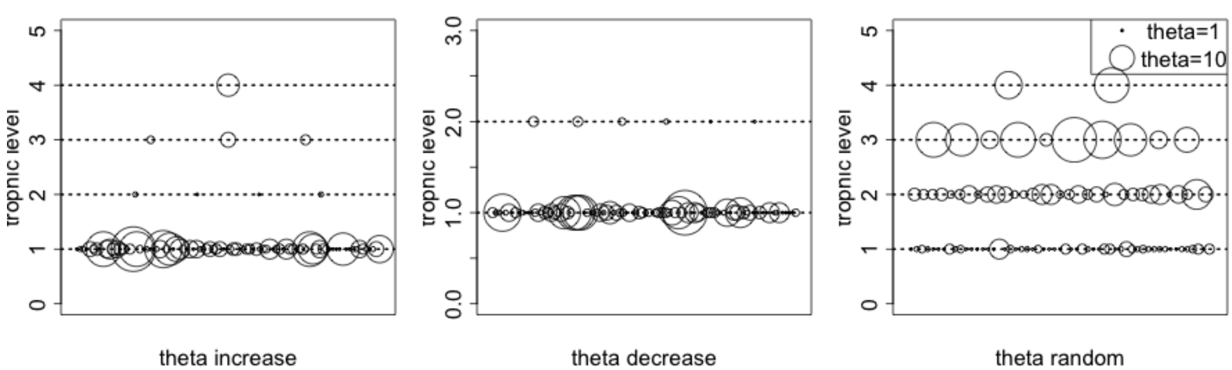

Figure 3. a) Food web structure, before trophic leaps ($D_r = 0.7$)

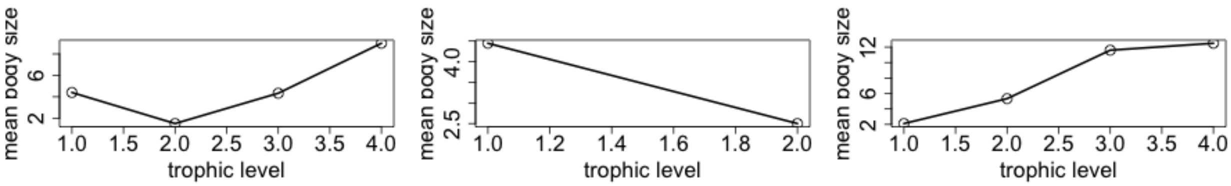

Figure 3. b)Mean body size variation across trophic level, before trophic leaps ($D_r = 0.7$)

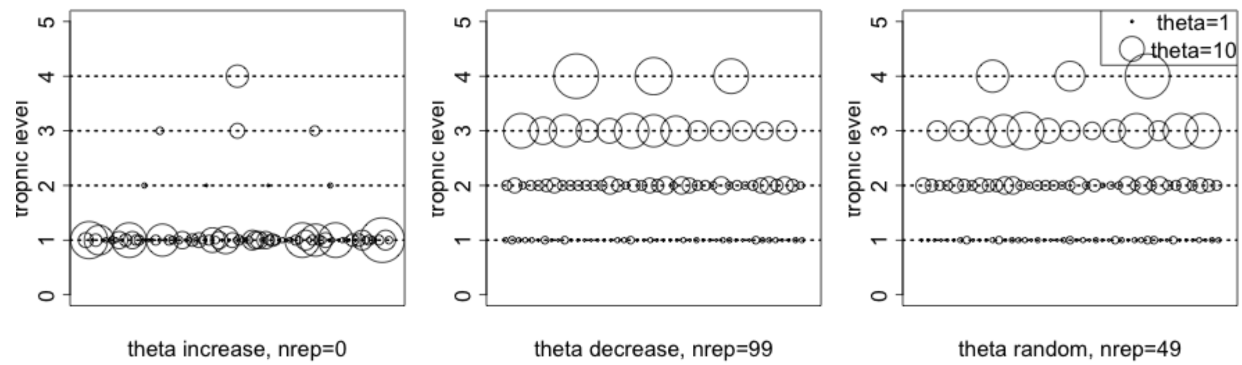

Figure 3. c) Food web structure, after trophic leaps ($D_r = 0.7$)

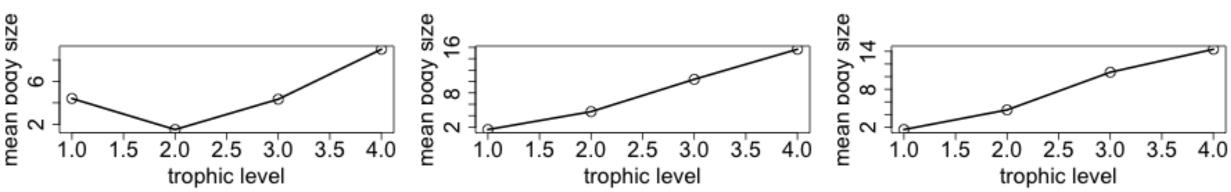

Figure 3. d) Mean body size variation across trophic level, after trophic leaps ($D_r = 0.7$)

3.4 $D_r = 0.9$

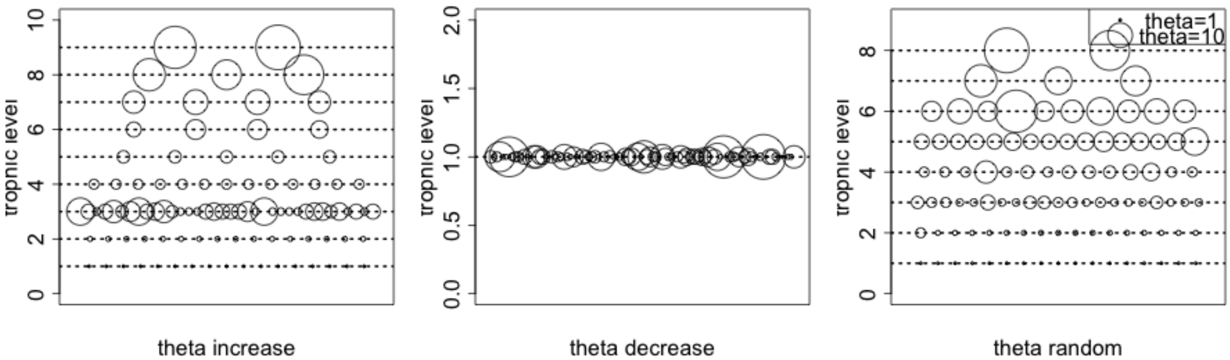

Figure 4. a) Food web structure, before trophic leaps ($D_r = 0.9$)

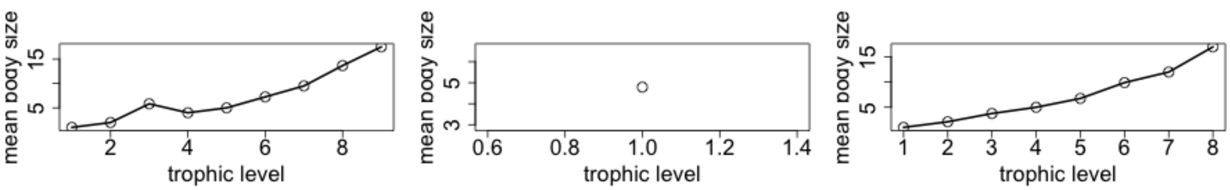

Figure 4. b) Mean body size variation across trophic level, before trophic leaps ($D_r = 0.9$)

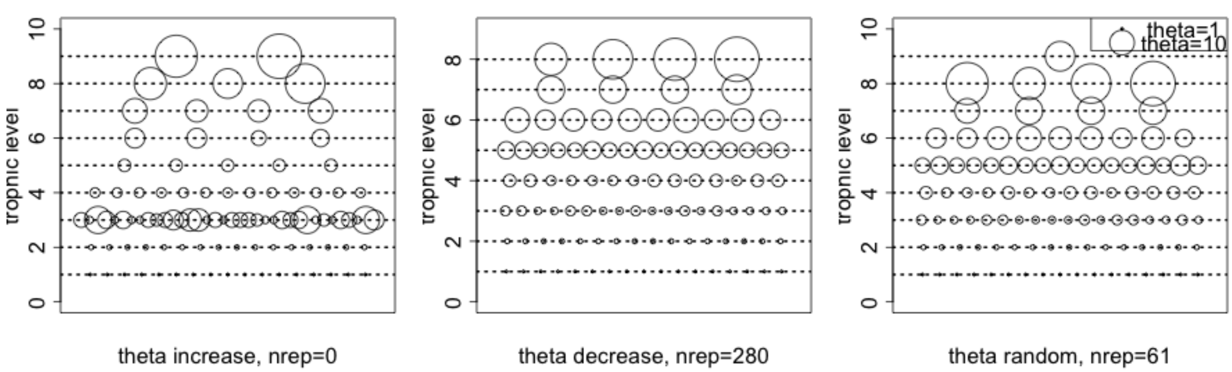

Figure 4. c) Food web structure, after trophic leaps ($D_r = 0.9$)

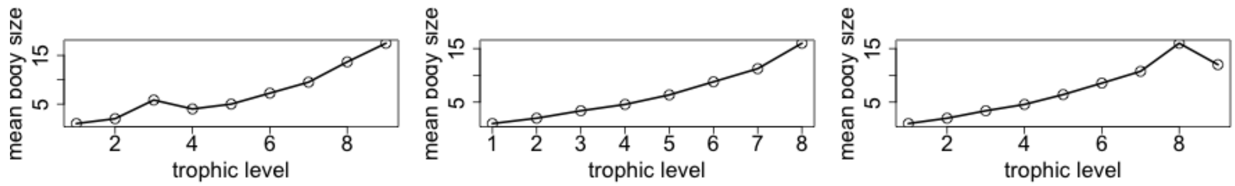

Figure 4. d) Mean body size variation across trophic level, after trophic leaps ($D_r = 0.9$)

4 Discussion

From the graphs we can see that:

I. Although the number of trophic levels before trophic leaps is affected by the sequence in which species are added, it is the same for all sequences after trophic leaps.

This means that the number of trophic levels in the long term (when trophic leap is possible) might be solely determined by D_r (a universal value for all species) given the total number of species and the body size distribution among the species, regardless of the sequence in which species are added. Reversely applying this relationship provides a way to determine a community-wise D_r from the number of trophic levels.

II. The body size increasing sequence gives the most stable food web structure through time, where the least number of trophic leaps is needed after species enter the community.

The number of trophic leaps for the increasing case is 0 except for $D_r = 0$ (nrep $= 1$). Analytical derivations are needed to precisely prove it. For an intuitive explanation, since D_r is held constant for all species, the only parameter that affects comparative advantage between species is θ. According to the analytical solution of MERA, a species with a smaller θ has higher competitive advantage than a species with a bigger θ. Therefore when a new species is added into a trophic level, it is more likely for a species with a bigger θ from that level to be outcompeted and become motivated for trophic leaps compared to a species with a smaller θ. Based on this, the increasing case is the most stable one because the bigger species are always added later than the smaller ones, creating less motivation for trophic leaps in general.

III. After trophic leaps, the body size decreasing case and the random case generate very similar structures while the increase case generates a distinct structure, indicating the possible existence of multiple stable structures for the food web in the long term.

The result shows that there are at least two alternative stable structures for the food web given the species composition, the first corresponding to when species are added strictly following a body size increasing sequence, the second corresponding to a random sequence or body size decreasing sequence. From graph d) we can see that for the first stable structure, the mean body size of species within a trophic level does not vary monotonically with trophic level (the lowest mean body size could be corresponding to a medieval trophic level) while for the second state, the mean body size increases monotonically with the trophic level. Specifically, the meadow example seems to be a realization of the first stable structure, where the herbivore (insects) as a medieval trophic level has the smallest mean body size.

Again more precise theoretical and empirical support is needed but intuitively, adding species in a body-size-increasing sequence could be the case from several different perspectives. First, bigger species evolved later than smaller ones in general. From an ecological point of view, smaller species are usually better colonizers (r strategy with higher abundance) and therefore more likely to arrive at a new community earlier than bigger species.

In the future, further analyses are needed to reveal if there are additional stable structures in-between the two we have identified, and how reshuffling the sequence in which species are added lead to transition from one stable structure to another.